EVOLUTION IN A DETERMINATE LINE AS ILLUSTRATED BY THE EGG-CASES OF CHIMÆROID FISHES.

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Recent attempts to explain evolutional processes, whether, *e. g.*, by natural selection, orthogenesis or use-inheritance, have been based, with but few exceptions, upon parent and offspring, in the direct relation of one to the other. Thus, (1) in the newly developed field of biometrics, variations in parent and offspring, have been discussed in terms of precision; (2) in embryology and embryopathology, ingenious experiments have tested the latent possibilities of the offspring at different stages in its career, and (3) on the side of paleontology, variations of progeny and parents have been examined on a giant scale in terms of survival and obliteration of masses of individuals. On the other hand observations are scanty, even in the present outburst of literature, which test the relation of the young to its parents by *indirect* means. This is, none the less, a line of inquiry which bids fair to become a fruitful one. And we may even at the present time consider what materials can be obtained which shall provide a series of parallel changes between the offspring and, *e. g.*, *some other product* of the parent, and through such means furnish, as it were, a *point d'appui* for evolutional studies. Thus: Are there any means of ascertaining whether an animal in providing for its progeny can produce structures *which form no organic part of the young yet which at the same time indicate accurately what the young will need in the distant future. And if these structures do occur, are they sometimes so special in their nature that they cannot be interpreted as general provision for the embryo, but rather for the late and complicated needs both of the genus for which they are provided and even of the species?* Obviously the parent has physical continuity with its young, but has it more than this? Has it the power to anticipate accurately the needs of the young, which it abandons and with whose subsequent fate it

clearly has nothing to do? Can it, for example, start an egg on its course of development and then provide it with a capsule whose special structures shall "foresee" accurately what the young is to become? Can it form a capsule which shall have the power, in spite of its lifeless substance, to develop as the enclosed egg develops, so that at each period it can best serve the corresponding stage of the embryo's growth? Such instances, if they can be found, are evidently of value in the examination of the complex problems of heredity.

The following notes are given since they appear to illustrate an extreme case in point: and since they also indicate that somewhat similar "purposeful" conditions may be demonstrated in the secondary embryonic membranes of other forms, *i. e.*, that these structures may be found the better adapted to the *future* grade of development of an embryo than has hitherto been suggested.

In examining the shark-like fish, *Chimæra* (*C. colliei*), the egg-capsule was found to be specialized, *i. e.*, adapted for the embryo at a late stage of development, rather than for the egg, in the following characters (Cf. figures in BIOL. BULLETIN, 1903, Vol. IV., pp. 271, 272):

I. *In Size.* — The capsule is not fitted to the egg; in fact, the outline of the egg is squeezed into a long ellipse, in order that it may be contained in the case, for if the case be opened and the tension relaxed the egg regains its circular outline, and the capsule with its appendage is then much (about nine times) longer than the egg. The great size of the capsule (longer in proportion to the adult body than that of a single egg of any known animal) is in evident adjustment to the advanced development of the young fish at the time it is cast upon its own resources. In point of fact it is then well grown — about one fifth the length of the adult — and by this time it has entirely lost its yolk and resembles the parent in remarkable detail — in axial and appendicular skeleton, in fins, viscera, in dermal, even in secondary sexual characters, *e. g.*, clasping organs of male.

II. *In Shape.* — The capsule as laid down in the oviduct is divided into special regions destined to contain the snout, trunk and tail of the young (at time of hatching). In earlier stages

the egg was contained in but a single region (trunk region) of the capsule. In a word, the capsule is destined to fit the shape of the embryo when full grown as accurately, to seek for a comparison, as the mummy case its mummy.

III. *In Permanence.* — The development of the young *Chimæra* is slow, taking many months, perhaps a year in hatching. The capsule is adapted to future conditions in its shape and texture, enabling it to resist wear and tear as well as the softening action of the water. Its "life," in other words, corresponds with the duration of the embryo's period of incubation.

IV. *In Attachment.* — During its long service the capsule is insured against displacement and attendant injury by means of specialized structures. These include a definite stalk, long, tough, springy, and a disc- or bulb-shaped terminal, capable of durable attachment.

V. *In Position.* — Experiments with capsules containing eggs show that when there is even a slight movement of water the capsules, as they lie on the bottom, assume a position with the keel side upward. This is the side which is dorsal in the orientation of the embryo and which bears the lid through which the fish later escapes. Furthermore, the capsule is provided with a vertical and a pair of lateral expansions which, if a current of water is present, cause it to rotate like a weather-vane in the direction of the oncoming stream. By this means the young fish is adjusted to its respiratory current and at the same time protected against the injuries which would follow the continual dislodgment of the capsule.

VI. *In its Orientation with Respect to the Growing Embryo.*—The germinal disc and early blastoderm in about fifty capsules examined occupied a constant position with reference to the capsule, appearing on the keeled side, and when the young embryo could be determined the head always pointed in the direction of the large end, *i. e.*, the operculate end, of the case. The same position is maintained in later stages, the head directed toward the large end of the capsule, the tail gradually invading the narrow sheath-like end. Symmetry is maintained with reference to the sagittal plane of the capsule.

VII. *In its Arrangement Enabling the Imprisoned Embryo to*

Obtain a Circulation of Water. — This the capsule provides by means of an elaborate system of perforations. These are bilaterally arranged, one series situated directly above the future gill region of the embryo, and a second series in the sheath in which the tail develops. These rows of perforations, moreover, are graduated in size, suggesting that in certain regions the perforations are adapted to functional needs. The embryo causes a water current to enter above the gills and to pass out on either side of the tail. (Cf. the turning of the capsule against the current, like a weather-vane.) In this connection the writer notes that he has seen the embryo execute vigorously a rhythmic undulating movement of its greatly elongated tail, which, provided with a continuous dorsal-caudal and anal-caudal fin, can only be interpreted as a specialized organ for forcing the water backward through the case.

VIII. *In its Elaborate Provision for the Escape of the Embryo at Term.* — By a delicate adjustment of the folded dorsal wall of the capsule, a line of separation is formed in the respiratory perforations above the gill-region. Thus arises an opercular flap, which finally opens in a way which suggests the opening of the lamellar beak of a duck, and thus enables the young fish to escape. This arrangement is a remarkably complicated one, the valve being provided, among other things, with roll-over margins which preclude its being opened from without and so perfectly adjusted that it opens only to the necessary degree. Once opened, moreover, the valve margins cannot be restored in their former relations, thus indicating that a state of tension has existed, comparable somewhat to that of dehiscent seed capsules.

IX. *In the Progressive Changes in the Lifeless Substance of the Capsule which take place pari passu with the Developing Needs for these Changes on the Part of the Growing Embryo.* — At the time the capsule is deposited it admits no water to its interior. In fact, the unused tail sheath is then entirely filled with a plug of thick albumen. The perforations are formed by a process of weathering, during which delicate septa obstructing the openings are gradually broken down and thus a greater current of water is admitted to the interior of the capsule. In later stages these openings are largest and most numerous. By the same process

the opercular flap, *i. e.*, the opening valve, is prepared progressively, so that the embryo can escape in due time.

X. *In its Provision for the Latest Embryonic Characters in Different Species.* — The egg capsules of four species of *Chimæra* known to the writer, present distinctive characters, and among these are some which are prophetic of the structures of the adult fish. Thus the tail sheath of the capsule of *C. colliei* is thick and relatively short, fitting the tail of the embryo of a species in which no adult opisthure is noticeable: in *C. mitsukurii*, on the other hand, the opisthure of the adult is of extreme length, and the tail sheath of its egg capsule is correspondingly long and delicate. The egg cases of *C. phantasma* and *C. monstrosa* suggest correctly intermediate conditions in the adult opisthures.

To return to the theme of the present paper: A point of general interest presented by this complicated capsule is its bearing upon the factors of evolution. For, considering always that the substance of the capsule is only indirectly connected with the egg, *i. e.*, as a secretion formed by the parent after the mechanism of heredity has already been established in the egg, it nevertheless (1) "foresees" with startling exactness the size and shape of the young fish when many months hence it comes to hatch out, and (2) it provides a series of progressive modifications adapted to the developing physiological needs of the young. It is evident, accordingly, that if natural selection be adduced to explain the present phenomenon it encounters difficulties more numerous and complex than in usual instances. In the latter cases selection concerns itself with variations which affect the progeny directly; but in the present case variations must have occurred in the lines *both* of the progeny and, indirectly, of its far less individual capsule-forming capabilities — with the result that a succession of closely correlated steps in variation must have coincided in both distinct directions.

To make more apparent the complicated nature of this procedure an example might be devised in which numbers appear. Thus: At each point in the development of the young *Chimæra* let the number of important fortuitous variations be represented by 1,000 (which I think all will agree is a number of possibilities

modest rather than excessive). And let the same number of possible variations be present in each of the various stages in the development of the capsule. Accordingly, at the first stage let us grant that variation number 673 happened to be the most favorable one: this then was selected in both the embryo and in the capsular secretion; at the second step some number, *e. g.*, 973 was similarly selected in both; at the third, number 14 in both; at the fourth, number 467 in both; at the fifth, number 801 in both; and at the two hundredth, number 761 in both. In other words, if we reckon the progressive series as extending over but two hundred steps, taking this number merely for the sake of example, as the possibilities are multitude, the chances are obviously remote of establishing the foregoing coincidences in the two series (one representing the development of the egg, the other of the capsule) by constantly repeated selection of fortuitous and fluctuating variations. For, taking the first coincidence of a favorable fortuitous variation of the embryo selected by a favorable fortuitous variation in the capsule, or indeed, even a coincidence of variations which are passable, not optimum, in both, it is evident that we are dealing with an accident of an improbable character. Thus, for variation 673 of the embryo to have seized upon variation 673 of the capsule there is but one chance in a thousand. Granted, however, that this unexpected result happened: for the second optimum variations in egg and capsule to have coincided, say the number 973 in both, there is again but one chance in a thousand, — or in other words, the chance for coincidence in the favorable selection of the optimum fortuitous variations one and two, the chances would be one in a million; of variations one, two and three, one in a billion.

It would be urged, on the other hand, by selectionists that these figures are misleading, since with hosts of variations taking place in each stage of egg and capsule there would always be a coincidence of one favorable (although perhaps not the best) variation in the egg with a correspondingly favorable (perhaps not the best) character in the capsule. But this assumption leads to no essential change in the result, for in this case if the variations do not correspond with fair accuracy, at successive stages the embryo will not fit the conditions of the capsule, and

must accordingly perish.[1] In other words, in the first stage of variation, assuming again variations 1 to 1,000 in egg and in capsule, the chances for coincidence of even passable variations would be so small that a vast proportion of the embryos would fail to mature. And of the small number which did survive the first selection the majority would evidently be eliminated in the second stage of selection. For one egg, in short, to have run the gauntlet of the favorable variations in the capsule there must have been, and must still be an enormous proportion of failures.[2] The latter is evidently false, for it was found that the eggs of *Chimæra* are about as hardy and fruitful as the eggs of other sharklike fishes. Morever, if it is necessary to show still further the insufficiency of this selectionist argument, one need only reflect that nature would have to support millions of adult *Chimæra* in order that there might be laid one golden egg! The race, in short, could at the best have existed but a few generations in view of its slowness of breeding and the small number of eggs (possibly a dozen a year) laid by each female. But this inference is palpably false, for we know that the race of chimæroids has been producing specialized egg capsules from Jurassic times.

Natural selection of fortuitous variations is, accordingly, clearly valueless in explaining the evolution of the present capsule. Use and disuse also are to be eliminated as factors in its development. If a neo-Lamarckian suggests that the capsule is a result of use, having been primitively moulded *in utero* around the *full grown* young, one need only reply that such a suggestion is in itself anti-Lamarckian, for why would a capsule, let alone a complicated one, be formed at all when the embryo is so fully grown that it cannot need it, and why should elaborate provision for aquatic breathing be present in a uterine capsule? One need hardly offer

[1] Thus, the proper variation for the opercular lid can only follow the favorable variation for the respiratory pores in the capsule, and these again can only follow if the capsule is of a great size, definite shape, or durable structure. And, of course, as definite an order must be followed in the stages of the embryo. And finally, the accurate regulation of time between the two must coincide. Thus the breathing pores of the shell must not open too early or too late.

[2] Admitting that "favorable," rather than optimum variations could have been successfully selected. Even organic selection, it seems to me, reduces the difficulty only in unessential regards.

the objection that in uterine development the well known law is to reduce secondary membranes rather than to increase them.

The capsule of *Chimæra* must stand, I conclude, as an instance of evolution in a determinate direction. Unhappily, however, it gives no data by which the cypher of orthogenesis can be simplified.